Available online at www.sciencedirect.com

SCIENCE DIRECT®

Forest Ecology and Management 227 (2006) 1–13

Forest Ecology and Management

www.elsevier.com/locate/foreco

Review

The development of British Columbia's tree seed transfer guidelines: Purpose, concept, methodology, and implementation

Cheng C. Ying, Alvin D. Yanchuk *

BC Ministry of Forests and Range, Research Branch, 722 Johnson Street, Victoria, BC, Canada V8W 1N1

Received 6 December 2005; received in revised form 7 February 2006; accepted 7 February 2006

Abstract

The development of forest tree seed transfer research, guidelines, regulations and policy has a long history in Canada, as well as in many other parts of the world. While the implicit assumptions of what is involved in developing seed transfer limits, guidelines and policy are generally accepted, the scientific and biological processes that underpin their validity are not readily available to most foresters. We provide an overview of the historical and current technical approaches to the development of seed transfer in British Columbia, and the overall framework which incorporates key biological, statistical and administrative issues in regulating the movement of forest tree seed. An example of how seed transfer information is developed from field experiments to guidelines or limits is provided from the lodgepole pine provenance tests in BC. Seed transfer research as it relates to the movement of wild or seed orchard seed will need to factor in the complications being predicted with climate change. As such, seed transfer research will continue to evolve as field experiments mature, new tests are established, statistical approaches and geographic information systems improve, and climate prediction tools attain greater resolution.

Keywords: Seed transfer; Genecology; Seed zones; Climate change

Contents

* Corresponding author. Tel.: +1 250 387 3338; fax: +1 250 387 0046.
E-mail addresses: cying@telus.net (C.C. Ying), Alvin.Yanchuk@gov.bc.ca (A.D. Yanchuk).

0378-1127/$ – see front matter
doi:10.1016/j.foreco.2006.02.028

1. Introduction

Nearly 80 years ago, Thrupp (1927), a Canadian forestry scientist, published a paper titled ''Scientific Seed Collection'' in the Forestry Chronicle in which he cautioned against the indiscriminate use of seeds from different geographic origins. He referred to the tremendous range of environment occupied by such species as Douglas-fir (*Pseudotsuga menziesii*), and the large differences seen in hardiness and growth of various seed sources. One year later Bates (1928), in a paper delivered at the meeting of the Canadian Society of Forest Engineers, and published also in the Forestry Chronicle, called for regulating seed movement in reforestation, and in his words, ''It may appear an unpleasant thing to say, and no doubt certain commercial interests will object to my saying it, but it is, nevertheless, altogether probable that we in the United States have a right to look with suspicion on most Canadian forest tree seed, and you have the identical right to demand the use in Canada of 'home grown' seeds. There are undoubtedly many cases in which seed may be sent across the border with no harm whatever, but almost certainly the general outcome of a better knowledge of the matter will be to restrict the transport of seed to comparatively short distance.'' He also suggested the need to expand seed origin tests to address the above concern. Dr. Bates was an American forest scientist, and to our knowledge, was the first to explicitly call for restriction on seed transfer in published records in North America. His words are as relevant today as they were then.

In British Columbia (BC), the practice of restricting seed movement, voluntarily or regulated, has a long history. Records of its practice are scattered in government regulations and policy papers or buried in meeting minutes. Moreover, the scientific basis and reasoning behind seed transfer guidelines are dispersed in technical journals, which are not readily accessible or read by the majority of practitioners. In this paper we attempt to provide a background summary of the evolution and development of BC's seed transfer guidelines. We will give a brief historical account of different stages of their evolution, focusing on advances in scientific knowledge and analytical methods that have been used. As such, construction of seed transfer guidelines is a dynamic process with advances in scientific knowledge and practical experience, particularly in the context of global warming. We hope this review will help advance the understanding of the concept and process, in other words the science, behind BC's seed transfer guidelines.

What is a seed transfer guideline? The ultimate goal of reforestation is to establish plantations that can yield their genetic potential within the environmental limits of climate, weather and soil. To achieve this goal, we must quantify a 'match' of planting stock with environments where the trees are suitably adapted. Seed transfer guidelines are one such tool which facilitates achieving this goal. Administratively, the current seed transfer guidelines are a set of statements that delimit the geographic range bounded by latitude, longitude, and elevation, within which a seed source may be used for reforestation. Biologically, the above physiographic descriptors serve as surrogates for the physical environment (e.g., climate) within which seedlings can grow to their genetic potential. Moving seed beyond this limit may result in maladaptation; e.g., cold injury, drought and susceptibility to disease and insects causing growth loss or mortality. Provenance and progeny testing results have amply demonstrated that seed sources from different geographic locations of the species' distribution have different growth potential and ranges of site environments where they can grow well (e.g., Campbell, 1986, 1987, 1991; Parker, 2000; Rehfeldt, 1983b, 1984, 1988, 1989, 1994; Sorensen, 1992, 1994; Morgenstern, 1996). In this paper, we primarily discuss the development of wild-stand seed transfer guidelines. Adaptive differences between wild and orchard seed are likely to become different as breeding cycles advance, and the latter may require different sets of seed transfer guidelines. But the rationale for constraining their movement is the same for both.

2. BC's seed transfer guidelines: a brief historical account

The initial seed zones in BC were delineated only for Vancouver Island and the south coast mainland in the 1940s (BC Forest Service, 1946; Lester et al., 1990). We found no official or published record of the practice of seed transfer until 1962 when Haddock, a professor of the Forestry Faculty of the University of British Columbia, recommended a seed collection zone map for Douglas-fir (Haddock, 1962). The map delineated seven seed zones for both the coastal and interior form of the species based on general climate and geophysiological attributes within the species' distribution range (Fig. 1). As reforestation expanded into the interior, a province-wide seed zone map was constructed in the early 1970s; 67 zones were delineated as the basis to guide seed collections (Fig. 2). Delineation of these zones also incorporated the preliminary approximation of ecological classification of forest lands. However, we did not find or do not recall any official records or documents that mandated the use of these zones in terms of seed movement: like many silvicultural regulations of that period, these seed zones were used only as references aiding foresters' decisions on the use of seed sources. The size of reforestation programs before 1970 was small (annual planting only a few million seedlings) and the use of local seeds was a common practice.

Rapid expansion of the reforestation program in the 1980s, which reached over 200 million seedlings of annual planting (Cuthbert, 1990), required critical selection of seed sources in order to safeguard healthy and productive plantations. The advance of the biogeoclimatic classification (BEC) of forest land in the 1980s (Pojar et al., 1987) also indicated the necessity for some seed zone realignment. Moreover, results from the maturing provenance and progeny testing for major commercial species (Ying and Morgenstern, 1987) also supported the theoretical expectations that local populations are not necessarily genetically optimum (Namkoong, 1969). Convergence of these factors prompted a formal review of seed transfer guidelines and seed zones in 1983 jointly by Silviculture Branch and Research Branch of BC Ministry of

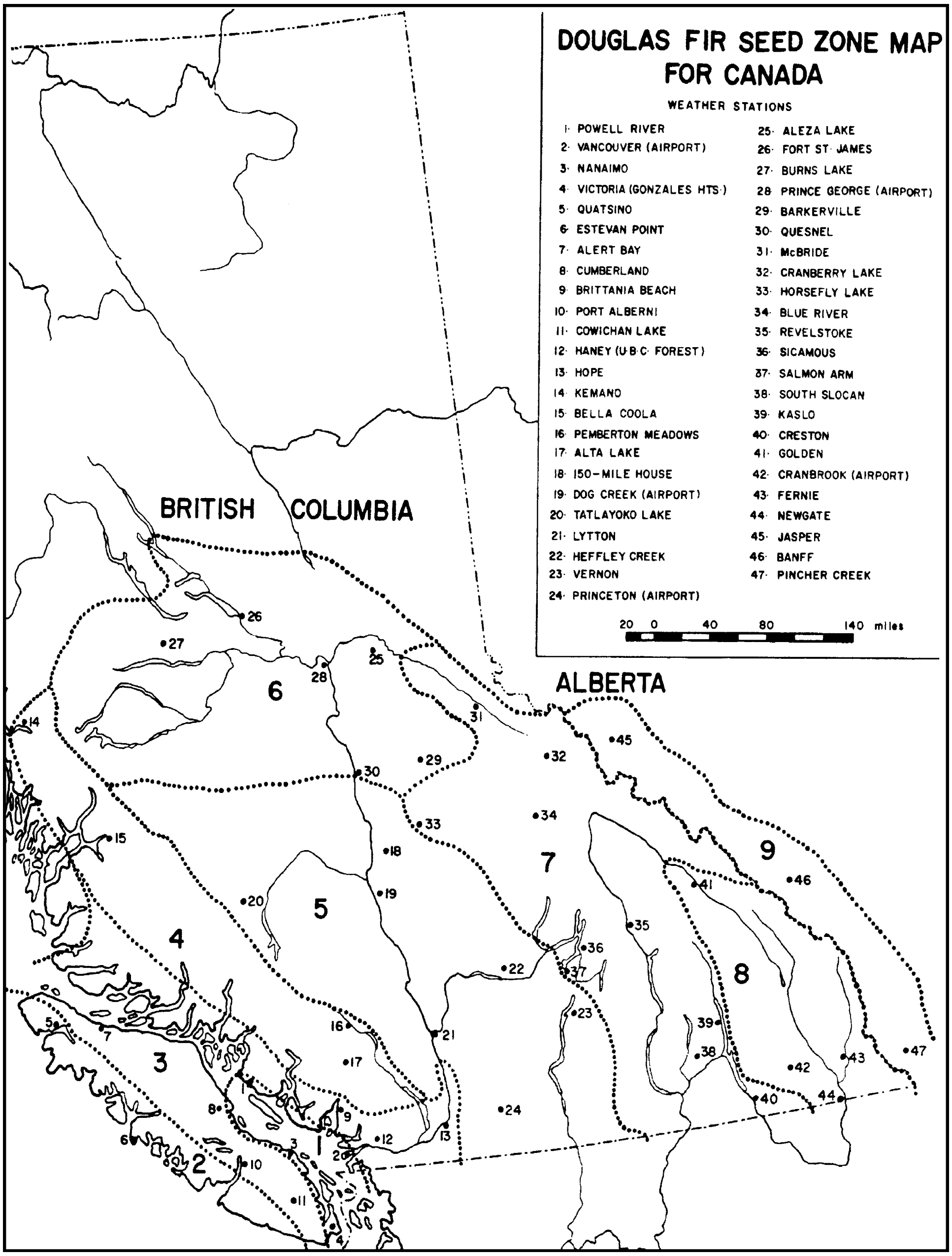

Fig. 1. Haddock's (1962) seed zone map for Douglas-fir (probably the first published seed zone map in BC).

Forests. Jenji Konishi (then Manager of Forest Seed Production) led the review, and a task force was formed consisting of seed orchard managers, forest geneticists, ecologists, and silviculturists from both industry and government. The review started with interior species, expanded to coastal species and resulted in the reduction of seed zones from 67 (Fig. 2) to 24 (Fig. 3), and incorporated the notion of 'floating principle' of seed transfer (Rehfeldt, 1983a) as the principal means of regulating seed transfer. The latter allows the transfer of a seedlot beyond zone boundaries as long as it is within its adaptive limit.

BC's seed transfer guidelines have not evolved in isolation. Increase in knowledge of genetics and ecology of tree species, and the development of new analytical approaches in other regions has impacted their evolution. Below we give an overview of two major advances in concept and analytical approach, which have significantly impacted the changes in BC's seed transfer approaches in recent decades.

2.1. Fixed-boundary zone

Delineations of contiguous fixed-boundary seed zones are typically the first steps in regulating seed transfer (Morgenstern, 1996), as they were in British Columbia. In this approach, large administrative regions are delineated into seed zones that are relatively environmentally uniform, and seed transfer (i.e., deployment of planting stock) is restricted to the zone in which it was procured. Seed zone delineation and boundaries largely

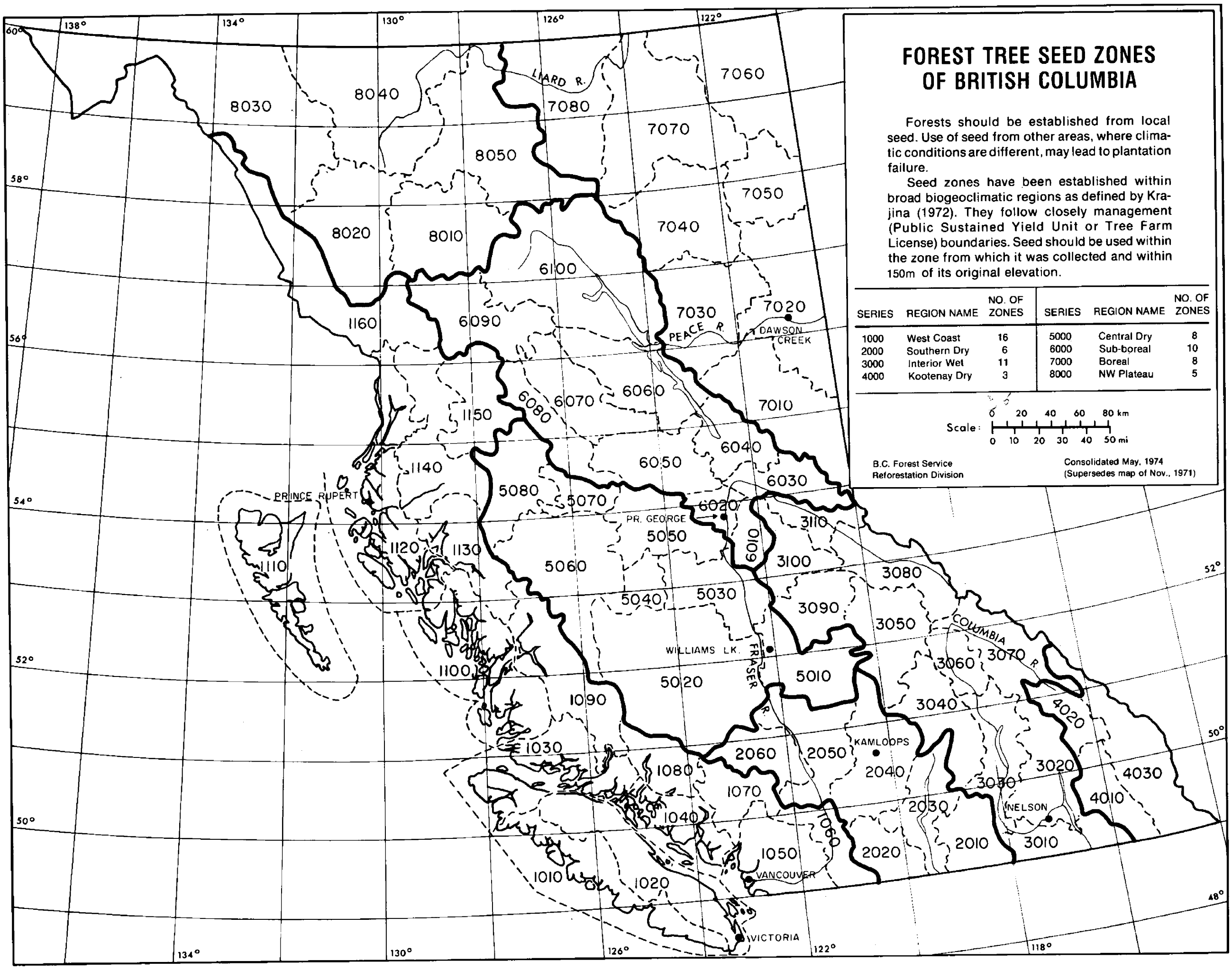

Fig. 2. The first official seed zone map in BC 1974–1982.

remained a qualitative and descriptive exercise until Campbell's (1974) pioneering work brought a modelling concept into zone delineation.

Campbell (1974) employed a regression approach to scale zone size, a milestone approach that shifted zone delineation from a descriptive and qualitative (pattern-recognition) to a quantitative and predictive (process-seeking) approach. One tenet assumption in Campbell's modelling concept was that local adaptation varies clinally across the landscape, that is, if climate varies clinally, adaptive traits should vary likewise. The assumption considers natural selection as the dominant force in the formation of the observed pattern of adaptive variation across the landscape (Campbell, 1974, 1976, 1983, 1986, 1987). His concept was largely rooted in the theory of niche-partition, a prevailing concept in the 1960s and 1970s (May and MacArthur, 1972), which translates into genotype-niche matching (Campbell, 1979, 1987). With application of his concept of local adaptation to seed transfer, relative risk increases with increasing phenotypic distances between two populations regardless of their directions, and thus risk of maladaptation increases in their displacement (e.g., Campbell, 1976). Campbell's conceptual approach in seed zone delineation is a conservative one seeking to ensure planted trees are genetically similar to local trees, with an implicit objective to preserve landscape genetic adaptability, rather than a utilitarian approach that considers improving site productivity as a component in seed transfer. The latter would require results from substantial long-term field testing. He recognized his zones were provisional (all seed zones are provisional) without the benefit of long-term testing results. His approach would naturally result in smaller zones, when phenotypic distances are translated into geographic distances (Campbell, 1983). Campbell's contribution rests with its conceptual originality; advances in approaches in seed transfer and their analytical methods in recent decades are extensions of Campbell's conceptual framework.

2.2. Floating seed transfer

Rehfeldt (1983a) introduced the 'floating principle' into seed transfer. Both the floating principle and Campbell's fixed-boundary zone use the same analytical approach of regression models delimiting the transfer distance or zone size according to the steepness of the adaptive clines along

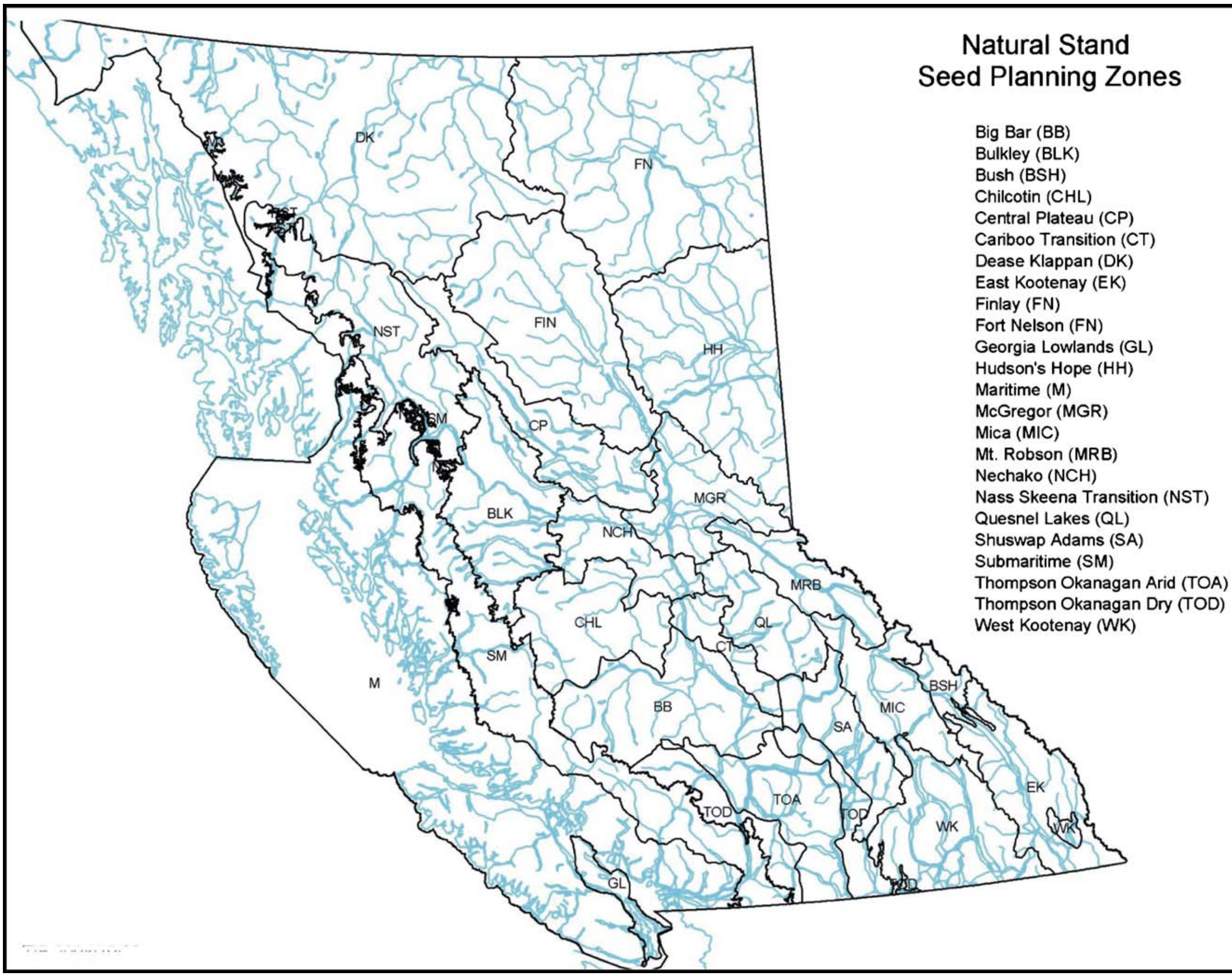

Fig. 3. The current seed planning zone map in BC 1988-present (boundaries modified several times).

geographic gradients, as determined by regression models (the steeper the cline the narrower the transfer distance or zone size). However, all seed transfer limits will 'float' to some degree depending on the origin of seed sources along the clines. The floating principle also recognizes that similar genotypes tend to occur in similar environments. For example, similar genotypes occur at different elevations as geographic distances in latitude and longitude change (i.e., a population at some lower elevation at a higher latitude can be similar to a population at a high elevation but at a lower latitude). Therefore, floating transfer can be discontiguous. Rehfeldt termed floating seed transfer as "seed zone without boundary." Since patterns of adaptive differentiation among commercial tree species in BC are predominately clinal, floating transfer is biologically conducive. Another significant advantage of the floating transfer approach is that it provides flexibility in operational seed transfer, and is now the primary criteria in guiding the use of natural seeds in reforestation in BC (BC Ministry of Forests, 2004). Dr. Jerry Rehfeldt, in his prolific career, has refined, broadened and integrated the Campbell concept with evolutionary biology and ecological principles, and in particular, extended its practical application globally.

3. Construction of seed transfer guidelines: a conceptual framework

Regulating seed transfer in reforestation is practised in one form or another in all major forest regions in the world, but the scientific concepts behind these guidelines or regulations are rarely described in their entirety. In this section, we attempt to outline the conceptual and scientific basis for BC's seed transfer regulations.

3.1. Pattern and process

The essence of natural sciences is an exercise of pattern-recognition and process-seeking, which is a fundamental concept in the development of seed transfer guidelines. We first observe and establish the pattern of a natural phenomenon, from which we analyse, infer and test its causative process, and then quantify the pattern–process in a predictive model (Watt, 1947; May, 1986; Levin, 1992). An observable pattern can be ephemeral, but the process that governs the formation of pattern is 'perpetual'. A predictive model that is anchored in the understanding of the process that drives the pattern formation usually carries higher predictability than the one that stands alone on pattern. This is the fundamental motivation for investing so much effort in testing, data collection and careful analysis.

Provenance testing provides the scientific basis for construction of operational seed transfer guidelines. Provenance research, a derivation of the classical common-garden adaptation study of plant species pioneered by Turesson (1922), seeks to identify patterns and processes (Callaham, 1964; Wright, 1976; Morgenstern, 1996). In provenance testing, provenances are sampled in a systematic manner across the species' entire range, or across a segment of its natural range of specific interest, and tests are established in a series of scientifically designed field tests in natural or semi-natural conditions. The test sites are typically distributed along geographic gradients, where we observe and measure patterns of responses. We then correlate provenance responses with climate variables or their surrogates in latitude, longitude and elevation of provenance origin. A significant correlation suggests a causative process of natural selection across the environmental gradient; the stronger the correlation the stronger the effects of natural selection (i.e., we have quantified the process) (Thorpe, 1987). Scientific verification of pattern–process relationships of a natural system, such as provenance variation – natural selection, in the classical sense of experimental repeatability is not feasible. We can only infer it from statistical tests. Mayr's (1956) principle of 'pluralism', that is, convergence of such correlations among different species further provides the rationale to accept such pattern–process correlations. Provenance literature has unequivocally demonstrated such convergence (e.g., Campbell, 1974, 1986, 1991; Rehfeldt, 1983b, 1984, 1988, 1989; Sorensen, 1992, 1994; Ying et al., 1985). Other evolutionary forces such as gene flow (Slatkin, 1987; Wu and Ying, 2004), genetic drift (Endler, 1983), and historical events (i.e., origins of the founder population) (Thorpe, 1987), can reduce or constrain the effectiveness of natural selection. However, natural selection is the ubiquitous force (Linhart and Grant, 1996) and thus serves as a plausible benchmark in measure against other forces.

3.2. Fitness and fitness trait

From the evolutionary perspective, by limiting seed movement, seed transfer guidelines help to ensure that planted trees are 'fit', that is, they are adapted to their planted environments (Ayala, 1969; Wallace, 1989; Mitchell and Valone, 1990). Three fitness components – capability to cope with changing environment, capability to compete, and capability to reproduce – together guarantee the survival and thus perpetuity of wild tree populations. However, 'fitness of a plantation', in order to capitalize on site productivity for wood production, requires only the capacity to cope with a changing environment in the short-term (i.e., a harvesting rotation). Also, inter-genotypic competition is reduced by controlled densities or spacing, and generally they do not need to attain reproductive maturity. This is the utilitarian view of fitness and adaptation (Mangold and Libby, 1978), and suggests 'plantation fitness' is less stringent. Regardless, fitness of a seed source that is used to grow a plantation is obviously critical, and so is the choice of a proper trait that we can effectively use as a surrogate of fitness. Total height is commonly used as a fitness trait in delineating transfer limits. A common concern is 'do growth traits represent a proper measure of fitness?' We believe they do.

First, a large part of the variation in site index as expressed in height in natural stands is genetic (Monserud and Rehfeldt, 1990). Second, growth vigour confers adaptive advantages in both capacities of reproduction (i.e., a taller tree has a better chance to flower and produce seed) (e.g., Ying and Illingworth, 1985) and competition (a taller tree is a better competitor for light, soil moisture and nutrients) (e.g., Mitchell and Goudie, 1980). Third, the first response of tree species to changing environment (e.g., warming climates) is likely to be in height growth, which in turn confers reproductive advantage (Gamache and Payette, 2004).

Dobzhansky (1956) and Mayr (1983) advised using a focal trait that reflects the fitness of a whole organism. Ecophysiological properties of tree height as described above seem to well fit their concept of a focal trait. Height growth, as a focal fitness trait, accommodates the utilitarian view of fitness, and does not severely compromise a plantation's long-term fitness, in case the plantation is used for purposes other than short-term wood production.

3.3. The scale factor

The scale at which seed transfer is regulated is important because the mechanism that drives the process in pattern formation varies depending on the scale on which the pattern of a natural phenomenon is observed (Levin, 1992). Construction of operational seed transfer guidelines must consider patterns of variation at a proper scale that can be measured with reasonable accuracy in relation to causative processes (i.e., quantitatively predictable by a model). They also cannot excessively burden the implementation. A biologically perfect seed transfer guideline that is burdensome in implementation is not a functional one. In Levin's (1992) words, "To develop the predictive models that are suitable for a management purpose, we must learn how to aggregate and simplify, retaining essential information without getting bogged down in unnecessary details that pertain to the chosen scale." "Unnecessary details" do not mean they are not important; rather they are difficult to incorporate into a predictive model without excessively burdening its implementation. Therefore, the scale factor impacts seed transfer in both its science and its implementation.

BC seed transfer is regulated on broad regional scale. Once this choice of scale is made, we are committed to implement the guideline in accordance with geographic patterns of provenance variation that are rooted mainly in a climate-driven process (e.g., Rehfeldt et al., 1999; Wu and Ying, 2004). The effect of factors not associated with the chosen scale such as slope aspect, soil, etc. have to be treated as "unnecessary details". In fact, edaphic factors have been shown not to be particularly important relative to most of the adaptive genetic variation in Douglas-fir (Monserud and Rehfeldt, 1990;

Campbell, 1991). The relevance of the scale concept will become evident when we illustrate the construction of operational seed transfer and its implementation.

3.4. Optimization

Construction of operational seed transfer limits is conceptually an optimization process, which may be done in different ways but subject to constraints, both biological and non-biological. Crowe and Parker (2005) propose the use of non-parametric models as an optimization tool aiding decision on the number of zones on the prospective of balancing cost and benefit (site productivity). O'Neill and Aitkin (2004) adopt the concept of zone size-maladaptation correlation and use cluster analysis to optimize zone size with minimizing in-zone maladaptation as the criterion. Hamann et al. (2000) use the combination of redundancy analysis and kriging (geostatistics) to delineate zones of optimal seed sources. The traditional approach of Parker's (e.g., 1992) focal-zone, Rehfeldt's (e.g., 1990) floating transfer, and Campbell's (e.g., 1979) fixed-boundary zone employ regression-type models to delineate transfer distance or zone size with the statistical limit of local optimality. The common thread in these diverse approaches is optimization.

Interestingly, optimization is an industrial concept employed to quantify profitable allocation of resources to better industrial operation against standard procedures at the time, and was later brought into evolutionary biology as a quantitative tool to measure natural selection and its efficiencies (Maynard Smith, 1978; Parker and Maynard Smith, 1990). If natural selection were the sole factor affecting adaptation and fitness, we would expect local populations to be 'optimal' (i.e., most fit). As stated earlier, local optimality is often not observed because other evolutionary forces such as gene flow (Slatkin, 1987; Wu and Ying, 2004), adaptational lag (Matyas, 1990), random drift, and historical events (i.e., founder population) can constrain the effectiveness of natural selection (Namkoong, 1969; Thorpe, 1987).

When optimization is employed in construction of operational seed transfer rules, the analysis first requires a benchmark measure, like a standard measure of production against which industrial optimization is measured. It is plausible to assume local optimality as the benchmark, and a statistical model is then constructed to quantify the degree of departure from this benchmark, as the basis to delineate the transfer in both direction and distance. For the transfer of wild-stand seed we are in a sense 'correcting' for the degree of non-local optimality. For improved seed, we aim to correct for non-optimality as well as increase the overall growth potential.

4. Construction of seed transfer guidelines: empirical framework and implementation

Science is increasingly playing an important role in regulating natural resource management, but practical knowledge and experience – the 'art' – remains a significant component of the process. In British Columbia, the interplay of 'science and art' makes the construction of operational seed transfer limits a trade-off system among three guiding principles: (1) enhance plantation productivity, (2) minimize biological risk of adaptation, and (3) accommodate administrative and planning realities of reforestation programs.

4.1. Seed planning zones

As indicated earlier, provenance testing has shown genetic variation is predominantly clinal in most of our BC native species, and so floating transfer is the principal process used to guide the use of natural seeds. Fixed-boundary seed zone is auxiliary to floating seed transfer in cases such as regulating transfer across significant climate and ecological boundaries, e.g., from moist to dry zones. Otherwise, the zones (called seed planning zones, Fig. 3) function mainly as units for administrative and planning purposes such as ordering seed, tracking seed inventory, auditing planting stock, etc.

The zone boundary is basically an overlay of adaptive genetic variation on top of the ecological classification of forest lands. BC's forest land classification is a hierarchical classification of zone, sub-zone, and variant based on the synthesis of geography, climate, and vegetation patterns, called biogeoclimatic classification (BEC) (Pojar et al., 1987).

Effectiveness of BEC-provenance variation overlay is evaluated with the aid of different statistical models. In the case of lodgepole pine, regression models with BEC sub-zone variants as explanatory variables accounted for as much variation among provenances and among test sites as models using latitude, longitude and elevation as explanatory variables (Wu et al., 2005; Hamann and Wang, personal communication). This indicates geographic patterns of provenance and site variation, though clinal, parallel BEC zones rather well. So an overlay of genetic variation with BEC in boundary delineation is biologically compatible, and also simplifies administration. For example, species' selection guidelines, implemented prior to seed transfer guidelines in reforestation, are entirely tied to BEC classification. As well, feedback from genetic analyses can help fine-tune inter- and intra-specific variations with BEC sub-units. Both are dynamic, and modifications are made whenever additional information can justify them.

4.2. Floating seed transfer

At the core of floating seed transfer is a predictive model. The higher the model's capacity to capture the pattern–process connection of provenance variation, the higher the reliability of the model's output on which the direction and distance of floating transfer is delineated. Statistical approaches in model construction vary depending on available data, and scale and design of provenance testing that generate the data. We use the approach of Wu and Ying (2004) for lodgepole pine to illustrate model construction. We present only a simplified version of their modelling procedures and model output, primarily to show how the asymmetrical distances in floating transfer were derived.

First, a one-dimensional component quadratic response function in a three-dimensional space of latitude, longitude and elevation for each test site is derived. For example, for the derivation of the component quadratic response function along latitude, it can be expressed as

$$Y(x_1 : x_2, x_3) = a + bx_1 + cx_1^2$$

where Y is the provenance means of 20-year height, x_1 the latitude of provenance origin and x_1^2 its quadratic form, and x_2 and x_3, the longitude and elevation of the test site where the derived response function applies. So mathematically, it is a quadratic response function for the latitudinal component under the constraint of holding longitude and elevation the same as the test site. In the same manner, component response functions can be derived for longitude and elevation. These functions characterize the variation pattern among a range-wide sample of ~60 provenances tested at each site, and from these quadratic functions, we estimate 20-year heights of local and optimal populations as illustrated in Fig. 4. The analysis was done separately for each of the 57 test sites.

Second, local optimality as a measure of the degree of optimality of the local population relative to the optimal population in both distance and direction, is defined. Fig. 4 illustrates this definition. D-Lat is the distance in degrees between local and optimal populations along latitude, a measure of degree of optimality of the local population (the larger the distance, the less optimal the local population). Local optimality in direction depends on the position of the optimal population in relation to the test site (local population): positive D-Lat indicates the optimal population is located south of the site (as shown in Fig. 4) and negative D-Lat north of the site. Assigning the + and − sign to D-Lat facilitates recognition of the physical position of optimal population. Fig. 4 illustrates that the optimal population is located at 2° of latitude south of the site, which is a surrogate for their biological difference in 20-year height. This conversion from biological to physical distance is needed because we cannot directly apply the former in operational seed transfer.

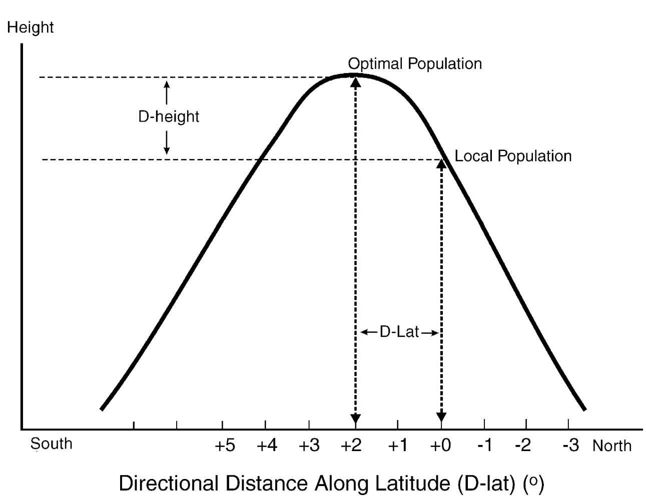

Fig. 4. Graphical illustration of directional distance (D-Lat) estimated from the quadratic response functions along latitude: positions of optimal (peak of the curve) and local populations, and distance between them (D-Lat). Positive D-Lat indicates the optimal population located south of the test site.

In the same way, the degree and direction of local optimality along longitude (D-Long) and elevation (D-Elev) are defined. Positive D-Long indicates the optimal population is located east and negative west of the sites, and positive D-Elev the optimal population is below and negative above the sites. D-Lat, D-Long and D-Elev with positive and negative designation measure local optimality in both distance and direction in relation to the optimal population. We term them directional distances (Fig. 4). These directional distances were then used in correlation analyses with latitude, longitude and elevation of the test sites to establish geographic patterns of local optimality. The results essential to the decision on asymmetrical transfer in direction and distance are summarized in Fig. 5.

Third, the key model output in geographic patterns of local optimality has to be interpreted. Fig. 5 shows the correlative patterns of local optimality (expressed as directional distance as defined above) with latitude (Fig. 5a), longitude (Fig. 5b) and elevation (Fig. 5c) across the test sites. Fig. 5 shows:

(i) *An asymmetry in the geographic pattern of local optimality*: a steep cline of local optimality along longitude (Fig. 5b), that is, the farther west (increasing longitude), the lesser the optimality of local populations (increasing distance between local and optimal population); a slightly smaller cline along elevation (Fig. 5c), that is, the higher the elevation, the lesser the local optimality; a milder one along latitude (Fig. 5a), that is, the farther north, the less optimal are local populations;

(ii) *An asymmetry in the position of optimal populations*: along longitude, optimal populations are located to the east at 85% of the sites (points above 0-line, Fig. 5b); along elevation, 79% are below the sites (Fig. 5c); along latitude, 70% are to the south of the sites (Fig. 5a);

(iii) *An asymmetry in distance between local and optimal populations*: along longitude, average distance of the optimal populations located to the east was 3.47° (average +D-Long above the 0-line), only 0.79° to the west (average −D-Long below the 0-line, Fig. 5b); for elevation, 357 m below (+D-Elev) and 98 m above (−D-Elev, Fig. 5c); but most evenly distanced along latitude, south 1.06° (+D-Lat) and north 1.05° (−D-Lat, Fig. 5a).

Fourth, the above output needs to be translated into a science-based seed transfer guideline for the species:

1) East-to-west along longitude, and low-to-high along elevation, being more critical than south-to-north in directional transfer in latitude ((i) and (ii)).
2) 3.5° westward and 1.0° eastward transfer along longitude; 350 m upward and 100 m downward along elevation; 1.0° both northward and southward along latitude (output (iii)).

For the floating transfer distances in (2), we use the average distances of departure of the optimal populations from the sites (the rounded-off averages of (ii)). From a purely statistical

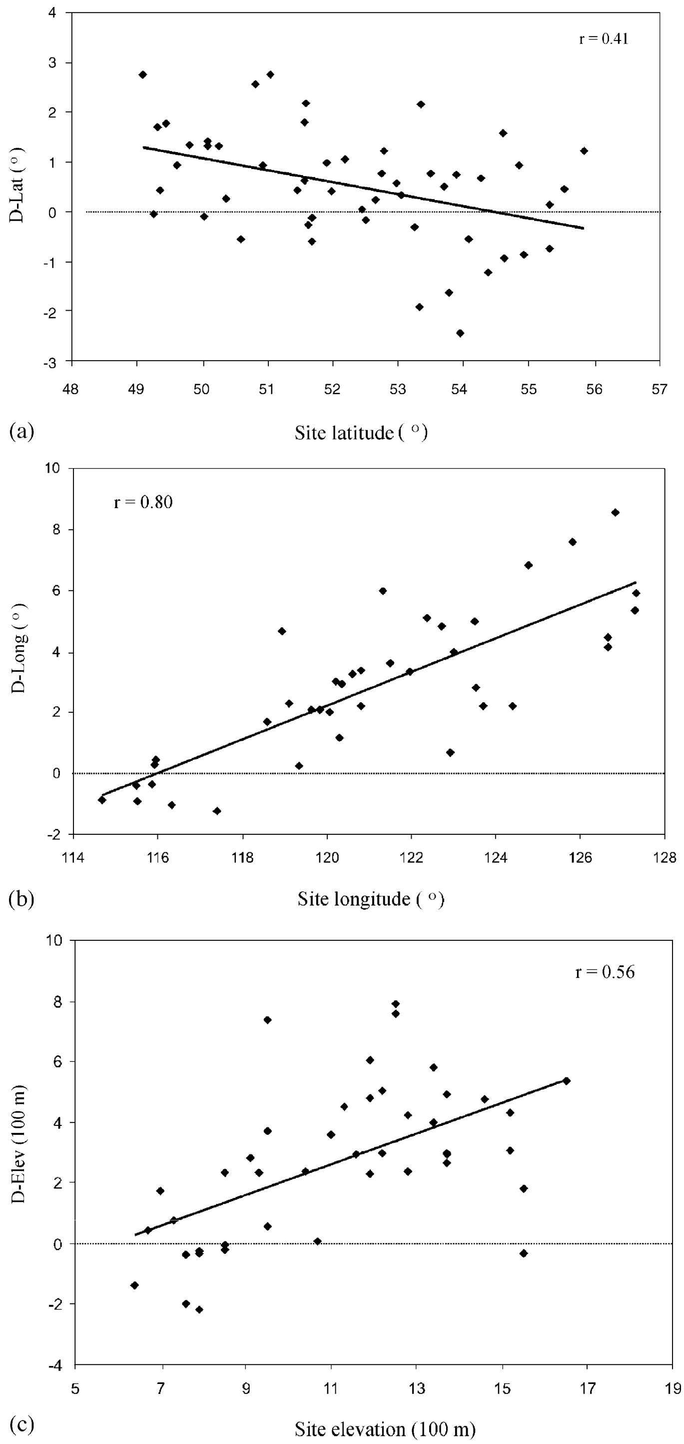

Fig. 5. Correlation of directional distances in latitude (D-Lat), longitude (D-Long), and elevation (D-Elev) with the test site latitude (a), longitude (b), and elevation (c). Positive D-Lat indicates optimal population located south and negative north of the site, positive D-Long east and negative west of the site, and positive D-Elev below and negative above the site.

viewpoint, the floating distances would vary according to the specific locations of the planting sites along latitude, longitude and elevation. For example, along longitude, towards the east where optimal population tends to be relatively close to the site, only local seed source should be planted. We should then progressively increase the distance of transfer from east toward the west to improve productivity; however, this would complicate the transfer guideline to the extent of impossible implementation. Floating transfer using the average distances of (ii) captures the asymmetrical nature of local optimality and simplifies its implementation. Different measures can be used to scale floating distance and zone width. Campbell (1979) and Sorensen (1992) used additive genetic variance, and Rehfeldt (1990) and Parker (1992) used LSD (least significant difference). Both produce symmetrical or mono-directional transfer, but using either will lose the asymmetrical nature in local optimality.

Wu and Ying (2004) concluded that the interplay of natural selection and directional gene migration functions as the causative process driving the formation of the observed pattern of local optimality. The former is due to relaxed selection pressure along the climate gradient from the continental northeast towards the milder southwest with considerable maritime influence, and the latter the counteractive effect of directional gene flow from shore pine (*Pinus contorta*. var. *contorta*) (Critchfield, 1957). Shore pine is known to be not well adapted to the colder interior environments. This interplay may have created adaptational lag (Matyas, 1990), causative to the observed asymmetric geographic pattern of local optimality. The asymmetrical transfer described above reflects, in a way, a correction of this adaptational lag, and is thus unlikely to incur adaptive risk.

4.3. Consultation

Consultation is one of the final steps where we integrate 'art' and science to form the operational version of the seed transfer rules or guidelines. The purpose is to seek broad input from foresters, forest managers, seed planners, and scientists on the practicability of the guidelines (the operational 'reality check'). Particularly important is that consultation provides the opportunity to incorporate local knowledge and experience. Predictive models, despite all the scientific effort, cannot always cover all potential situations across large forested landscapes. For example, there can be the thermal gradients along elevation in the more northern latitudes; temperature decreases with increases of elevation, particularly during the summer, but temperature increases with elevation during the winter months because of the strong radiation cooling effect from the long hours of darkness (Nyland, 1980). The above concern resulted in a much restricted elevational transfer for lodgepole pine north of latitude 56° (Appendix 3, BC Ministry of Forests, 2004).

For the central and southern interior (south of latitude 56°), the operational lodgepole pine transfer distances are: "latitude: 2° north and 1° south; longitude: 3° west and 2° east; elevation: 300 m upward and 100 m downward". The guidelines embrace the scientific basis of asymmetrical seed transfer in favour of south-to-north latitudinal, east-to-west longitudinal, and low-to-high elevational transfer. These floating transfer distances were minor modifications to accommodate operational flexibility, e.g., 2° northward instead of 1° along latitude and 2° eastward instead of 1° along longitude as prescribed in (2).

4.4. Variance

Requests for exemptions (variances) from seed transfer guidelines are common, but for the most part these requests are mostly minor deviations, e.g., the only seed source available for replanting a cutting block is marginally beyond a seed transfer limit. At present these are addressed on a case by case basis, with the scientist with most knowledge and experience of the species being asked to quantify risks (e.g., expected loss of growth, or increased susceptibility to pests, disease or damage). This can be contentious. Mathematical models on which our seed transfer guidelines are based cannot embrace all the local details (Levin, 1992), as we have emphasized. In a majority of cases, exemption requests require judgement calls. For example, we know lodgepole pine is susceptible to heavy snow press, and judgement of such risk requires local knowledge of detailed local topography. In our view, the ultimate decision must reside with the responsible authority for stewardship issues in the area (e.g., in BC it is currently the Forest Service District Manager), who must weigh all the factors that may have gone into trees being planted outside the designated transfer limit.

5. Recent advances

The last several years have seen substantial efforts devoted to the development of climate-based models (e.g., Matyas, 1994; Rehfeldt, 1995; Rehfeldt et al., 1999; Andalo et al., 2005) out of concern about whether the current native and plantation populations can maintain their expected level of productivity under the various climate change scenarios predicted from global warming. Use of seed sources in today's reforestation that can be optimally adapted to some future climate is obviously the key to alleviate such concern. Thus seed transfer guidelines that timely incorporate the elements of climate change will be critical.

There have also been substantial efforts in exploring different mathematical functions, e.g., Cauchy (Raymond and Lindgren, 1990; Lindgren and Ying, 2000), Gaussian (Roberds and Namkoong, 1989), and Weibull (Rehfeldt et al., 2003) in construction of the predictive models. Another is in the statistical approaches to delineate the zones themselves; as mentioned earlier, Hamann et al. (2000) employ the kriging method (a geostatistical analysis) to delineate seed zones, and O'Neill and Aitkin (2004) developed the concept of minimizing ''in-zone adaptive risk'' as criterion in-zone delineation. Both will require further testing of their general applicability, as they are more mathematically complex and the parameters may not be as easy and conducive to biological interpretation and application as that derived from regression models.

On the application front, Parker (1992, 2000) was the first to incorporate GIS into his focal-zone seed transfer as a precise graphic illustration of the zone shape and dimension. GIS now adds a powerful visual component to seed transfer planning and administration. It also adds the potential to transform seed transfer into a customized service as its accessibility increases, particularly important when seed transfer is eventually delimited according to climatic rather than geographic distances.

6. Future challenges in seed transfer

An increasingly common question is, should we develop and apply climate distance-based guidelines in operational seed transfer now? With many such climate modelling capabilities, we may now have the capacity to construct such guidelines, but a number of additional factors will need to be considered. (1) The current effort of modelling the response of tree growth to climate change in BC using the provenance testing results, i.e., a 'space-for-time' substitute approach (Rastetter, 1996), has some limitations. For example, on coastal BC, moisture is not a limiting factor on tree growth under the contemporary climate, resulting in a space-model in which precipitation variables are either dropped or rendered less significant in statistical process. We have to ask, will the effect of precipitation be less critical in future climates on the coastal region, as the space-model would predict (Oreskes et al., 1994; Rastetter, 1996)? (2) Migration from the current guidelines based on physical distances to the one on climate distances would be time-consuming and costly. The 'redrawing' of seed zones using climate predictions, with assumptions and tools discussed earlier, may be easy relative to the necessary changes that would need to be made to the provincial seed planning, registration, administrative, mapping and tracking systems currently in place. In other words, technical changes must occur in step with the agencies' capability to put them into effect. (3) Although the global general circulation models have shown convergence of their predictions at larger scales, at present the most evident signal is the warming trend at high elevations and northern latitudes. Projection of other aspects of global warming, e.g., its magnitude, resolution at a provincial level, its spatial pattern and scale, and the rate of climate change, etc. are much less certain.

The cautionary points made above certainly do not suggest that we are not willing to accommodate what we know and expect will occur, particularly at some of the larger scales. However, effective measures will likely come from local experience and knowledge, not model-projected scenarios at broad scale. Woods et al.'s (2005) study on correlation between the epidemic of *Dothistroma* needle blight of lodgepole pine with increasing precipitation exemplifies the value of such local effort. They clearly established the correlation between increasing precipitation in recent decades and the disease epidemic, but it is equivocal whether this correlation reflects the consequence of a trend due to global climate change. The authors suggest reducing the planting of the host species, particularly at more susceptible sites in moist zones, would effectively mitigate such epidemic regardless of global warming being the causative factor or not.

Our current seed transfer guidelines, which emphasize northward transfer along latitude and upward transfer along elevation, have already incorporated an adaptive measure by planting seeds from warmer climates at cooler sites. While these current guidelines may in fact only be compensatory for the adaptational lag present in most populations, new plantations should benefit (i.e., improved growth) from a warmer climate if global warming continues, and involve little risk of compromising their adaptation if the warming trend ceases. Also, we can easily verify the adequacy of the current guidelines in terms of climate change by converting the physical to climate distances using readily available software such as ANUSPLIN (Hutchinson, 2005), or 'Climate BC' (Wang et al., 2006) and further fine-tune the guidelines using the physiographic framework without a substantial change to the regulatory or administrative system now in place. Although prudence seems to call for adaptive and mitigating measures to climate change to be incremental, and continued research efforts to expand our knowledge and sharpen the tools are necessary, it is clear that relatively soon a large paradigm shift will have to be made which will make seed transfer more solidly grounded on climate variation.

As we indicated earlier, these concepts can also be incorporated into the movement of seed orchard seeds, or the delineation of breeding zones (e.g., Lindgren and Ying, 2000; Parker, 2000). Parental trees in seed orchards are selected through cycles of progeny testing and genetic recombination specifically targeted at a geographic area (i.e., a deployment zone). As breeding cycles advance, it becomes increasingly difficult to link 'adaptedness' of advanced-generation parent trees to their wild ancestors. In this sense, the origin of the wild parents becomes irrelevant and it is the performance of a parent tree's offspring that should determine a deployment zone. Thus, analytical approaches employed by plant breeders in the context of 'genotype-climate interaction' using climatic data of test sites will likely be more suitable and more practical for the transfer (deployment) of seed orchard seed (Westfall, 1992).

7. Conclusions

BC has a long history in regulating seed transfer of tree species, which has evolved with the advance of scientific knowledge and operational experience. Science increasingly drives the process, which involves the concept of statistics, ecology, evolutionary biology and plant breeding. The conceptual framework that provides the scientific skeleton of operational seed transfer represents organization in the context of pattern and process, fitness traits, the scale factor, and optimization. Geographic patterns of provenance variation, sifted through the scientific framework, provide the empirical basis in construction of operational seed transfer. Although traits that provide suitable measures of fitness are debatable, we maintain that height growth is a key and proper fitness trait.

Though science drives the process, practical experience and knowledge (i.e., the 'art'), plays an equally significant role in forming the guidelines for their operational practicability and administrative capability and efficiency. A seed transfer guideline that is anchored in such a framework of scientific concept and methodology, and practical experience and knowledge is expected to be functionally realistic. BC's seed transfer practice is incrementally incorporating measures to ensure that seed sources used in today's plantations can cope with future climate equally well.

Acknowledgements

We would like to acknowledge the contribution of a number of colleagues who reviewed this article. Dr. Andreas Hamann of the University of British Columbia (now at the University of Alberta), Drs. Frank Sorensen, Jerry Rehfeldt, and Bob Westfall of USDA Forest Service, Dr. Harry X. Wu of CSIRO, Australia, and Drs. Greg O'Neill and Michael Stoehr of the BC Ministry of Forests' Research Branch. Editorial suggestions by the two anonymous reviewers helped greatly to improve the content and flow of the article. We would also like to recognize the leadership of Charlie Johnson and Jenji Konishi (both retired) of the BC Ministry of Forests in the development of the seed transfer guidelines.

References

Andalo, C., Beaulieu, J., Bousquet, J., 2005. The impact of climate change on growth of local white spruce populations in Quebec, Canada. For. Ecol. Manage. 205, 169–182.

Ayala, F.J., 1969. An evolutionary dilemma: fitness of genotypes versus fitness of populations. Can. J. Genet. Cytol. 11, 439–456.

Bates, C.G., 1928. Some problems of seed production, collection and distribution. For. Chron. 5, 17–29.

BC Forest Service, 1946. Cone collections. In: Reforestation Manual: With Instructions to Forest Officers on Seed Collections and Planting Practice, Economics Division, Victoria, BC, 2 pp.

BC Ministry of Forests, 2004. Chief Forester's Standards for Seed Use. Victoria, BC, 35 pp.

Callaham, R.Z., 1964. Provenance research: investigation of genetic diversity associated with geography. Unasylva 18, 1–12.

Campbell, R.K., 1974. A provenance-transfer model for boreal regions. Meddel. Norsk Institutt Skogsforskning 31, 544–566.

Campbell, R.K., 1976. Adaptational requirements of planning stock. In: Global Forestry and The Western Role. Permanent Association Committees Proc., Western Forestry and Conservation Association, Portland, Oregon, pp. 103–107.

Campbell, R.K, 1979. Genecology of Douglas-fir in a watershed in the Oregon Cascades. Ecology 60, 1036–1050.

Campbell, R.K., 1983. Procedures for determining the biological limits of breeding zones in the Pacific Northwest. In: Proceedings of the USDA Forest Service Forest Genetics Workshop, Charlottetown, South Carolina, pp. 24–33.

Campbell, R.K., 1986. Mapping genetic variation of Douglas-fir to guide seed transfer in southern Oregon. Silvae Genet. 35, 85–96.

Campbell, R.K., 1987. Biogeographical distribution limits of Douglas-fir in southern Oregon. For. Ecol. Manage. 18, 1–34.

Campbell, R.K., 1991. Soils, seed-zone maps, and physiography: guidelines for seed transfer of Douglas-fir in southeastern Oregon. For. Sci. 37, 973–986.

Critchfield, W.B., 1957. Geographic Variation in *Pinus contorta*. Mario Moors Cabot Foundation Publ. No. 3. Harvard University, Cambridge, Massachusetts, 118 pp.

Crowe, K.A., Parker, W.H., 2005. Provisional breeding zone determination modelled as a maximal covering location problem. Can. J. For. Res. 35, 1173–1182.

Cuthbert, J., 1990. The future of forestry in British Columbia. Keynote Speech. In: Joint Meeting of Western Forest Genetics Association and IUFRO Working Parties S2. 02-05, 06, 02 and 14, Douglas-fir, Contorta pine, Sitka spruce, and Abies Breeding and Genetics Resources, August 20-24. Olympia, Washington, USA 11 pp. Sponsored by Weyerhaeuser Co.

Dobzhansky, T.H., 1956. What is an adaptive trait? Am. Nat. 90, 337–347.

Endler, J.A., 1983. Testing causal hypotheses in the study of geographical variation. In: Felsenstein, J. (Ed.), Numerical Taxonomy. Springer-Verlag, Berlin, Heidelberg, pp. 424–443.

Gamache, I., Payette, S., 2004. Height growth response of tree-line black spruce to recent climate warming across the forest-tundra of eastern Canada. J. Ecol. 92, 835–845.

Haddock, P.G., 1962. Douglas-fir in Canada: Seed Collection Zones Based on Geographic Variation of Populations as Influenced by Climate. Faculty of Forestry, University of British Columbia, Vancouver, BC.

Hamann, A., Koshy, M.P., Namkoong, G., Ying, C.C., 2000. Genotype x environment interaction in *Alnus rubra*: developing seed zones and seed transfer guidelines using spatial statistics and GIS. For. Ecol. Manage. 136, 107–119.

Hutchinson, M.E., 2005. ANUSPLIN Version 4.3 (July 23, 2005, http://cres.anu.edu.au/outputs/anusplin.php).

Lester, D.L., Ying, C.C., Konishi, J.D., 1990. Genetic control and improvement of planting stock. In: Lavender, D.P., Parish, R., Johnson, C.M., Montgomery, G., Vise, A., Willis, R.A., Winston, D. (Eds.), Regenerating British Columbia's Forest. University of British Columbia Press, Vancouver, BC, Chapter 14, pp. 180–192.

Levin, S.A., 1992. The problem of patterns and scale in ecology. Ecology 73, 1943–1967.

Lindgren, D., Ying, C.C., 2000. A model integrating seed source adaptation and seed use. New Forest 20, 87–104.

Linhart, Y.B., Grant, M.C., 1996. Evolutionary significance of local genetic differentiation in plants. Ann. Rev. Ecol. Syst. 27, 237–277.

Mangold, R.D., Libby, W.J., 1978. A model for reforestation with optimal and suboptimal tree populations. Silvae Genet. 27, 66–68.

Matyas, C., 1990. Adaptational lag: a general feature of natural populations. In: Joint Meeting of Western Forest Genetics Association and IUFRO Working Parties, Douglas-fir, Contorta Pine, Sitka Spruce, and Abies Breeding and Genetic Resources. 20-24 August, Olympia, Washington 11 pp.

Matyas, C., 1994. Modelling climate change effect with provenance test data. Tree Physiol. 14, 797–804.

May, R.M., MacArthur, R.H., 1972. Niche overlap as a function of environmental variability. Proc. Nat. Acad. Sci. (U.S.A.) 69, 1109–1113.

May, R.M., 1986. The search for pattern in the balance of nature: advances and retreats. Ecology 67, 1115–1126.

Maynard Smith, J., 1978. Optimization theory in evolution. Ann. Rev. Ecol. Syst. 9, 31–56.

Mayr, E., 1956. Geographic character gradients and climatic adaptation. Evolution 10, 105–108.

Mayr, E., 1983. How to carry out the adaptationist program? The Am. Nat. 121, 324–334.

Mitchell, K.J., Goudie, J.W., 1980. Stagnant lodgepole pine. In: Proc. Res. Activities Meet., vol. 2. BC Ministry of Forests, Research Branch, Victoria, BC, pp. 1–30.

Mitchell, W.A., Valone, T.J., 1990. The optimization research program: tudying adaptations by their function. The Quart. Rev. Biol. 65, 43–52.

Monserud, R.A., Rehfeldt, G.E., 1990. Genetic and environmental components of variation of site index in inland Douglas-fir. For. Sci. 36, 1–9.

Morgenstern, E.K., 1996. Geographic Variation in Forest Trees: Genetic Basis and Application of Knowledge in Silviculture. University of British Columbia Press, Vancouver, BC, Canada, 209 pp.

Namkoong, G., 1969. The non-local optimality of local races. In: Proceedings of the 10th Southern Conference on Forest Tree Breeding. Texas Forest Service, Texas A and M University Press, pp. 149–153.

Nyland, E., 1980. Lodgepole pine in Yukon. In: Proceedings of the *Pinus contorta* as an Exotic Species, IUFRO Working Party Meeting on *Pinus contorta* Provenances, Garpenberg, Sweden, pp. 27–43.

O'Neill, G.A., Aitkin, S.N., 2004. Area-based breeding zones to minimize maladaptation. Can. J. For. Res. 34, 695–704.

Oreskes, N., Shrader-Frechete, K., Belitz, K., 1994. Verification, validation, and confirmation of numerical models in the earth science. Science 263, 641–646.

Parker, G.A., Maynard Smith, J., 1990. Optimality theory in evolutionary biology. Nature 348, 27–33.

Parker, W.H., 1992. Focal point seed zones: site specific delineation by geographic information systems. Can. J. For. Res. 22, 267–271.

Parker, W.H., 2000. Rates of change of adaptive variation in *Picea Mariana* visualized by GIS using a different systematic coefficient. New Forest 20, 259–276.

Pojar, J., Klinka, K., Meidinger, D., 1987. Biogeoclimatic ecosystem classification. For. Ecol. Manage. 22, 119–154.

Rastetter, E.B., 1996. Validating models of ecosystem response to global change. Bioscience 46, 190–198.

Raymond, C.A., Lindgren, D., 1990. Genetic flexibility – a model for determining the range of suitable environment for seed source. Silvae Genet. 39, 112–120.

Rehfeldt, G.E., 1983a. Seed transfer in the northern Rocky Mountains. In: Proceedings of the USDA Forest Service Forest Genetics Workshop, Charlottetown, South Carolina, pp. 1–26.

Rehfeldt, G.E., 1983b. Adaptation of *Pinus contorta* populations to heterogeneous environments in northern Idaho. Can. J. For. Res. 13, 405–411.

Rehfeldt, G.E., 1984. Microevolution of conifers in the northern Rocky Mountains: a view from common gardens. In: Lanner, R.M. (Ed.), Proceedings of the eighth North American Forest Biology Workshop, Logan, Utah, pp. 32–46.

Rehfeldt, G.E., 1988. Ecological genetics of *Pinus contorta* from the Rocky Mountains (USA): a synthesis. Silvae Genet. 37, 131–135.

Rehfeldt, G.E., 1989. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*): a synthesis. For. Ecol. Manage. 28, 203–215.

Rehfeldt, G.E., 1990. Adaptability versus zone size: continuous zones for the Rocky Mountains (USA). In: Joint Meeting of Western Forest Genetics Association and IUFRO Working Parties, Douglas-fir, Contorta Pine, Sitka Spruce, and Abies Breeding and Genetic Resources, 20–24 August. Olympia, Washington 11 pp.

Rehfeldt, G.E., 1994. Evolutionary genetics, the biological species, and the ecology of the interior cedar-hemlock forests. In: Baumgartner, D.M., Lotan, J.E., Tonn, J.E. (Eds.), Interior Cedar-Hemlock-White Pine Forests: Ecology and Management. Spokane, Washington, pp. 91–100.

Rehfeldt, G.E., 1995. Genetic variation, climate models and the ecological genetics of *Larix occidentalis*. For. Ecol. Manage. 78, 21–37.

Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., Hamilton Jr., D.A., 1999. Genetic responses to climate for *Pinus contorta* in British Columbia: niche breadth, climate change, and reforestation. Ecol. Monogr. 69, 375–407.

Rehfeldt, G.E., Tchebakova, N.M., Milyutin, L.I., Parfenova, E.I., Wykoff, W.R., Kouzmina, N.A., 2003. Assessing population responses to climate in *Pinus sylvestris* and *Larix* spp. of Eurasia with climate-transfer models. Eurasian J. For. Res. 6 (2), 83–98.

Roberds, J.H., Namkoong, G., 1989. Population selection to maximize value in an environmental gradient. Theor. Appl. Genet. 77, 128–134.

Slatkin, M., 1987. Gene flow and the geographic structure of natural populations. Science 236, 787–792.

Sorensen, F.C., 1992. Genetic variation and seed transfer guidelines for lodgepole pine in Central Oregon. USDA For. Serv. Pacific NW Res. Sta. Res. Pap. PNW-RP 453. 30 pp.

Sorensen, F.C., 1994. Genetic variation and seed transfer guidelines for Ponderosa pine in the Ochoca and Malheur National Forests of Central Oregon. USDA For. Serv. Pacific NW For. Res. Sta. Res. PNW-RP-468. 30 pp.

Thorpe, R.S., 1987. Geographic variation: a synthesis of cause, data, pattern and congruence in relation to subspecies, multivariate analysis and phylogenesis. Bull. Zool. 54, 3–11.

Thrupp, A.C., 1927. Scientific seed collection. For. Chron. 3 (2), 8.

Turesson, G., 1922. The genotypical response of plant species to the habitat. Hereditas 3, 211–350.

Wallace, B., 1989. One selectionist's perspective. The Quart. Rev. Biol. 64, 127–145.

Wang, T., Hamann, A., Spittlehouse, D.L., Aitken, S.N., 2006. Development of PRISM based scale-free climate data for western Canada. Int. J. Climat. 26, 383–397.

Watt, A.S., 1947. Pattern and process in the plant community. J. Ecol. 35, 1–22.

Westfall, R.D., 1992. Developing seed transfer zones. In: Fins, L., Friedman, S.T., Brotschol, J.V. (Eds.), Handbook of Quantitative Forest Genetics. Kluwer Academic Publishers, Chapter 9, pp. 313–398.

Woods, A., Coates, K.D., Hamann, A., 2005. Is an unprecedented Dothistroma needle blight epidemic related to climate change? Bioscience 55, 761–769.

Wright, J.W., 1976. Introduction to Forest Genetics. Academic Press, New York, 463 pp.

Wu, H.X., Ying, C.C., 2004. Geographic pattern of local optimality in natural populations of lodgepole pine. For. Ecol. Manage. 194, 177–198.

Wu, H.X., Ying, C.C., Ju, H.O., 2005. Predicting site productivity and pest hazard in lodgepole pine using biogeoclimatic system and geographic variables in British Columbia. Ann. For. Sci. 62, 31–42.

Ying, C.C., Illingworth, K., Carlson, M., 1985. Geographic variation in lodgepole pine and its implication for tree improvement in British Columbia. In: Baumgartner, D.M., Krebill, R.G., Arnott, J.T., Weetman, G.F. (Eds.), Lodgepole Pine: the Species and its Management. Cooperative Extension Service, Washington State University, Pullman, WA, pp. 45–53.

Ying, C.C., Illingworth, K., 1985. Variation in cone and seed production from natural stands, plantations, and clone-banks of lodgepole pine, in: Shear, R.C. (Ed.) Proc. of the Conifer Tree Seed in the Inland Mountain West Symp. USDA Forest Service, Int. Res. Sta., Gen. Tech. Rep. INT203, pp. 191–199.

Ying, C.C., Morgenstern, E.K., 1987. The status of provenance research in Canada. In: Proceedings of the 21st CTIA Meeting. Part 2. Symposium on Tree Improvement – Progressing Together, August 17–21, Truro, Nova Scotia, pp. 1–19.